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Free Axial Lobes: An Important Diagnostic Character in *Pteridium* (Dennstaedtiaceae)

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Abstract

The overall form of the lamina in the bracken fern (*Pteridium*) is a fractal series in which blade, pinnae, pinnules and pinnulets represent a hierarchy of repeated units of decreasing size. Distinctive lunate or semi-lunate lobes of laminal tissue between the divisions of the blade in an apical zone of some or all of its axes are an important diagnostic feature. These "free lobes" link *Pteridium esculentum* (G. Forst.) Cockayne subsp. *esculentum* from Australasia with *P. esculentum* subsp. *arachnoideum* (Kaulf.) J.A. Thomson from Central and South America and separate both from *P. aquilinum* (L.) Kuhn. The development, pattern of distribution on laminal axes and variation of form of the free lobes in *P. esculentum* subsp. *esculentum* are described here. Although basic frond architecture as reflected in pinna spacing on the rachis is largely independent of the size of the lamina, the number and pattern of occurrence of free lobes is significantly correlated with the length of axial intervals and hence with frond size and laminal dissection. Attention is drawn to the likelihood that a genetic polymorphism may underlie development of free lobes in *P. esculentum* subsp. *arachnoideum*. The presence or absence of free axial lobes may be a useful marker for detection of introgression following hybridisation of *P. esculentum* and *P. aquilinum*.

Introduction

The abundant cosmopolitan bracken ferns (*Pteridium* Gled. ex Scop.) with a diploid (2n = 104) chromosome complement group on many morphological and molecular features into two distinct clades (Der et al. 2009, Thomson 2012, Zhou et al. 2014, Wolf et al. 2015) between which there is evidence of reproductive incompatibility (Brownsey 1989, Thomson and Alonso-Amelot 2002, Thomson 2012). One of these clades comprises *P. aquilinum* (L.) Kuhn, predominantly from the northern hemisphere and Africa, considered to include 11 (Thomson 2004, 2008, 2012) or fewer (Zhou et al. 2014) subspecies. The second clade comprises *P. esculentum* (G. Forst.) Cockayne with two subspecies of predominantly southern hemisphere distribution, namely *P. esculentum* subsp. *esculentum* in south-east Asia, Australia and New Zealand and *P. esculentum* subsp. *arachnoideum* (Kaulf.) J.A. Thomson in Central and South America (Thomson 2012, Zhou et al. 2014). Although treatment of the diploid bracken ferns as only two species appears to be emerging as a consensus, this view is not universally accepted: Schwartsburd et al. (2014), for example, argue for retention of the name *P. arachnoideum* at specific rank.

Hybrids between *P. esculentum* s.l. and *P. aquilinum* s.l. have been recognised in two geographic regions where these taxa overlap in distribution. *P. semihastatum* (Wall. ex J. Agardh) S.B. Andrews is an allotetraploid

(4n = 208) between *P. esculentum* subsp. *esculentum* and *P. aquilinum* subsp. *wightianum* (Wall. ex J. Agardh) W.C. Shieh in South-East Asia/Australia while *P. caudatum* (L.) Maxon is an allotetraploid hybrid of *P. esculentum* subsp. *arachnoideum* with *P. aquilinum* (subspecies not identified) in Central and South America (Thomson and Alonso-Amelot 2002, Der et al. 2009, Zhou et al. 2014, Wolf et al. 2015). There is evidence in both of these cases that hybrids or introgressants other than the allotetraploids are also present (Brownsey 1989, 1998, Wolf et al. 2015), meriting additional cytological, molecular and morphological analysis.

The presence in *P. esculentum* s.l. and absence in *P. aquilinum* s.l. of two characters concerned respectively with the abaxial indumentum and laminal subdivision have been widely used as diagnostic of these taxa (e.g. Tryon 1941, Mickel and Beitel 1988, Mickel and Smith 2004, Thomson 2012). One of these critical characters is the presence of minute highly distorted hairs termed gnarled trichomes (Thomson and Martin 1996, Thomson and Alonso-Amelot 2002, Schwartsburd et al. 2014, Wolf et al. 2015) between veins on the abaxial surface of laminal segments of *P. esculentum* s.l. If sufficiently dense, these hairs are seen at low magnifications as a surface texture that has been described as farinaceous (Tryon 1941, Schwartsburd et al. 2014), mealy (Brownsey 1989), or farinose (Schwartsburd et al. 2014). The density of gnarled trichomes is highly variable and strongly reduced in shade-form fronds of *P. esculentum* subsp. *esculentum* (Thomson and Martin, 1996) although hairs of this type were present in all of a large series of specimens of this subspecies examined to date. In contrast, *P. esculentum* subsp. *arachnoideum* from Brazil and Uruguay was observed to be polymorphic for presence/absence of gnarled trichomes (Thomson and Martin 1996, Schwartsburd et al. 2014).

The second character widely regarded as diagnostic of *P. esculentum* s.l. is the presence of "lunate or semi-lunate, entire lobes along part of the rachis, costae and costules, between the divisions of the blade" (Tryon 1941, p. 8). Such free lobes of laminal tissue are found proximal to the apices of the axes to an extent differing widely depending on growth conditions affecting frond size and subdivision. A detailed study of the pattern of occurrence and development of free lobes in a bracken population is presented here to facilitate field assessment and collection of material appropriate for taxonomic study, and to provide background for use of this character in revealing possible hybridisation or introgression.

Spacing of laminal elements on the frond axes

The evolutionary origins, patterns of development and diverse morphology of fern leaves have been extensively reviewed by Vasco et al. (2013). Unlike seed plants, fern leaves typically show determinate (finite) growth (Imaichi 2008) with prolonged acroscopic extension due to meristematic activity of a cell at the leaf tip. More proximal elements of the leaf thus mature first.

The overall form of the bracken lamina is that of a Mandelbrot fractal series (Thomson 2000) in which blade, pinnae, pinnules and pinnulets represent a hierarchy of repeated units of decreasing size. A general feature at each level in this series in *Pteridium* is the consistently greater spacing between basal lateral axes compared with those more apically (distally) placed, whether between pinnae on the rachis, pinnules on the costae, pinnulets on the costules or segments on the costulets (terminology following Lellinger 2002). Although visually distinguishable at each level, this pattern is most evident in the spacing of the costae (pinna axes) on the frond rachis.

The pinnae of *P. esculentum* subsp. *esculentum* are generally paired and opposite on the rachis, although quite frequently sub-opposite, apparently due to unequal elongation of the two sides of the rachis (O'Brien 1963). In analysing the spacing pattern of costae on the rachis care was taken to measure the distance between each successive costa from the base (Pinna 1) towards the apex on the same side of the rachis, but the pinna numbers used here each refer to a pinna pair whether exactly opposite or not. The distances between costae of pinna pairs P1 to P2, P2 to P3 … to P12 to P13 are shown in Figs 1 and 2 which illustrate a typical frond of subsp. *esculentum* 750 mm in height from a mixed dry sclerophyll woodland at Epping (Sydney, NSW). These spacings form an approximately exponential series decreasing from the base of the rachis (insertion of costa of P1) towards its apex beyond P13 (Fig. 2). Bright (1928) established that a similar gradation in spacing of pinnae on the rachis in *P. aquilinum* subsp. *aquilinum* is largely independent of frond size (height) by comparing the distances between successive pinna pairs relative to that between pinna 1 and pinna 2, standardised to a value of 1.0 for each frond. For comparison with Bright's analysis, pinna spacings P1 to P2, P2 to P3, P3 to P4 and P4 to P5 were measured for a sample of 30 fully expanded fronds of *P. esculentum* subsp. *esculentum* ranging in height between 565 mm and 1380 mm that were collected contemporaneously from the same site as the specimen illustrated in Figs 1-2. These fronds show a consistent pattern of pinna spacing on the rachis similar to that observed by Bright (1928) in subsp. *aquilinum*. When the distances between successive pinna pairs P1 to P2 through P4 to P5 are standardised with reference to the spacing of P1 to P2 taken as 1.0, the medians are respectively 0.53 for P2 to P3 (range 0.40 to 0.77), 0.40 for P3 to P4 (range 0.27 to 0.65), and 0.29

for P4 to P5 (range 0.2 to 0.4). In none of the fronds in the sample does the distance on the rachis between two successive pinna pairs exceed the spacing between the two next lower pinna pairs. Thus, although there is considerable variability between fronds, the overall pattern of pinna spacing is consistent from frond to frond after controlling for frond size. Experimental studies of fern leaf development (reviewed by Vasco et al. 2013) have established that the final shape of the fern leaf is determined by the pattern of division of the apical initial and of marginal meristematic and sub-marginal cells. Inhibition of cell groups positioned regularly along the marginal meristem of the developing leaf determines the spacing of the developing pinnae (Wardlaw 1963).
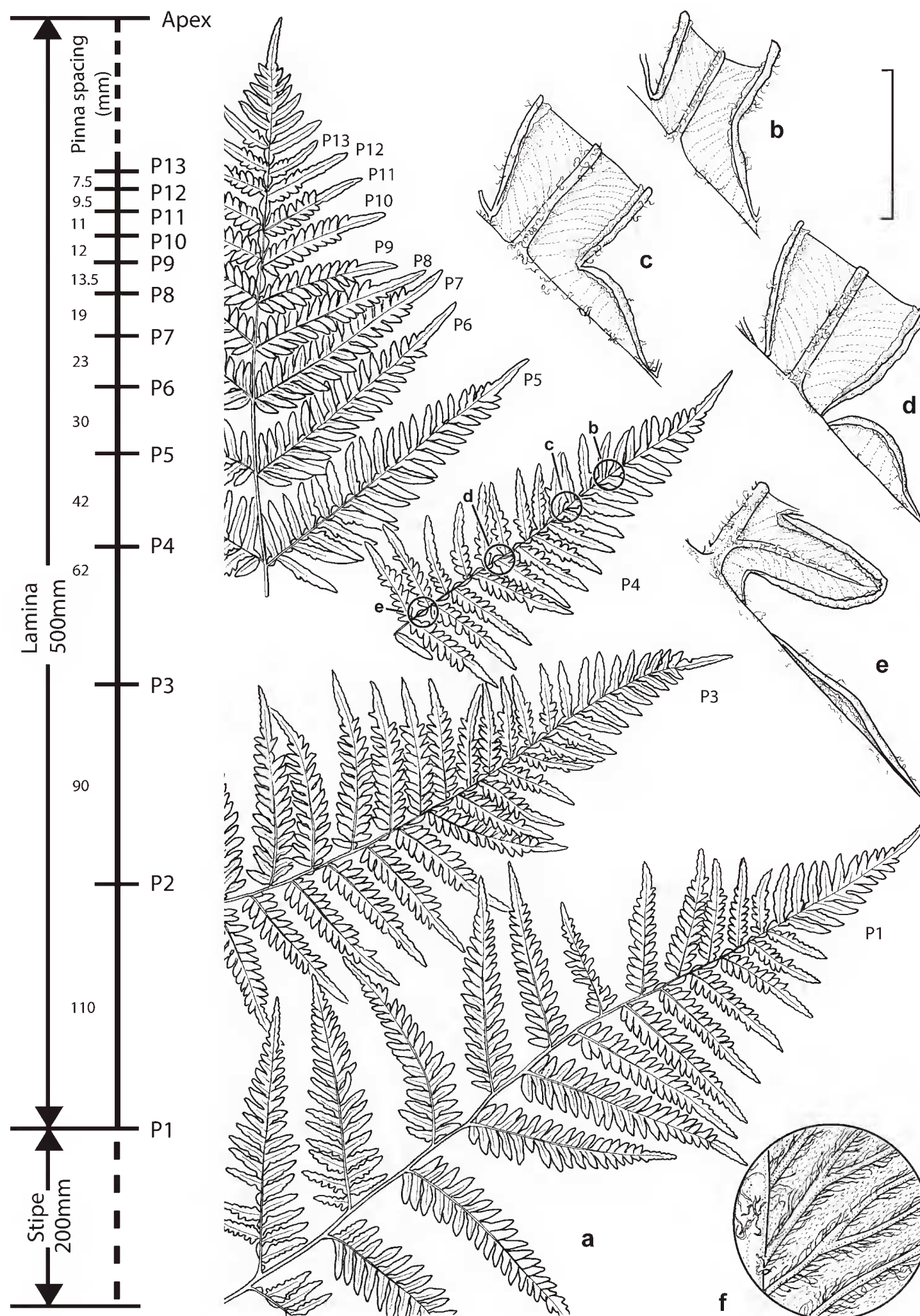

Fig. 1. Laminal dissection in a typical 3-pinnate to 3-pinnate-pinnatifid frond of *P. esculentum* subsp. *esculentum* from an exposed dry sclerophyll woodland site. **a.** Spacing of pinnae (mm) on the rachis is shown for the intervals between pinna pairs numbered acroscopically from the base of the lamina. One pinna (P) of each pair is shown removed from the rachis as P1, P3 and P4, while pinnae from P5 to the apex of the frond are shown in situ on the rachis. Note the reduced basal pinnule on P4. **b–e.** Different extents of separation of free lobes from decurrent segment bases along a pinna axis. **f.** Abaxial surface of a free lobe showing mealy appearance between veins at low magnification due to gnarled trichomes. Scale bar: **a** = 50 mm, **b–e** = 5 mm, **f** = 1.25 mm.

Origin, characteristics and position of free lobes

Proximal to the apices of the laminal elements in *P. esculentum* subsp. *esculentum*, segments may develop adnate decurrent bases that progressively lengthen to form a continuous narrow ledge on the side of the axis. This gives the appearance of "narrow wings on midribs of primary and secondary pinnae" (Brownsey 1989, see also Brownsey 1998). More frequently the apical segment bases gradually elongate and separate to form free lobes as illustrated for a pinna axis (costa) in Figs 1 b-d. Initially an indentation develops on the proximal side of a segment base close to the axis of that segment (Fig. 1b). In successive lobes down the axis, this cleft deepens and a gap opens on the axis as a more or less symmetrical semicircular lobe separates fully from its parent segment base (Fig. 1c). In a few of the more proximal axial intervals an elongated remnant of such a lobe forms a narrow flange on the side of the axis (Fig. 1d). In general, free lobes develop along both sides of the axial intervals over approximately 5-20 % of the length of the rachis just below the simple distal segments representing its apical pinnae (e.g. from P9 to P13 in Fig.1a), about 40% (P1)-70% (P3) of the length of the costae from a similar position but often along the full (P5), or nearly full (P4) length of the costae (Fig. 1a) as well as some basal intervals of costules (Fig. 1a, P1). Rarely, in the very largest 4-pinnate to 5-pinnatifid shade-form fronds (Fig. 3, and see below), free lobes are also present between a few of the most basal (proximal) laminal elements on the costulets. The contrasting absence of free lobes in *P. aquilinum* s.l. is illustrated for *P. aquilinum* subsp. *wightianum* (as *P. revolutum*) by Brownsey (1989, Fig. 2).

The distribution of the free lobes on laminal axes in *P. esculentum* subsp. *esculentum* varies widely, even between fronds of the same plant. The position (number from the base) of the most distal interval on each of these axes that carried free lobes, and the overall length of that axis from base to apex were recorded for a sample of 35 fronds. These specimens were collected at Epping (Sydney, NSW, same site as above) from a series of separate stands in a mixed dry sclerophyll woodland and are likely to represent a number of genets. The data are summarised in Table 1 where minimum, median and maximum values are shown. In each case the longer the axis overall, the further from its base is the axial interval carrying the lowest free lobe. The correlation between location of the lowest (most proximal) free lobe along the rachis and total rachis length is weak but significant (Spearman correlation coefficient, $r = 0.4214$, $P = 0.0117$). The correlation is stronger for the overall length of the basal costa and position of the most proximal free lobe along it ($r = 0.5924$, $P = 0.0002$) and for the overall length of the basal pinnule and location of its proximal basal free lobe ($r = 0.7915$, $P = 0.0001$). A large series of Herbarium specimens of subsp. *esculentum* from widespread localities in Australia and New Zealand shows patterns of free lobe distribution on the laminal axes consistent with those reported here.

Free lobes retain the characteristics of the ultimate segments which gave rise to them in relation to venation, the variable development of an apparently normal false indusium along the outer margin (Figs 1 b-e) and the presence/absence of gnarled trichomes between veins on the abaxial surface (Fig. 1f). Reflecting their origin as adnate segment bases, the veins of free lobes extend from the axis to which the lobe is attached to the outer margin of the lobe, i.e. at right angles to the lateral veins of the parent segment.

Table 1. Length of lamina, length of most basal pinna and length of most basal pinnule for a sample of 35 fronds of *P. esculentum* subsp. *esculentum* in relation to the most basal axial intervals carrying free lobes.

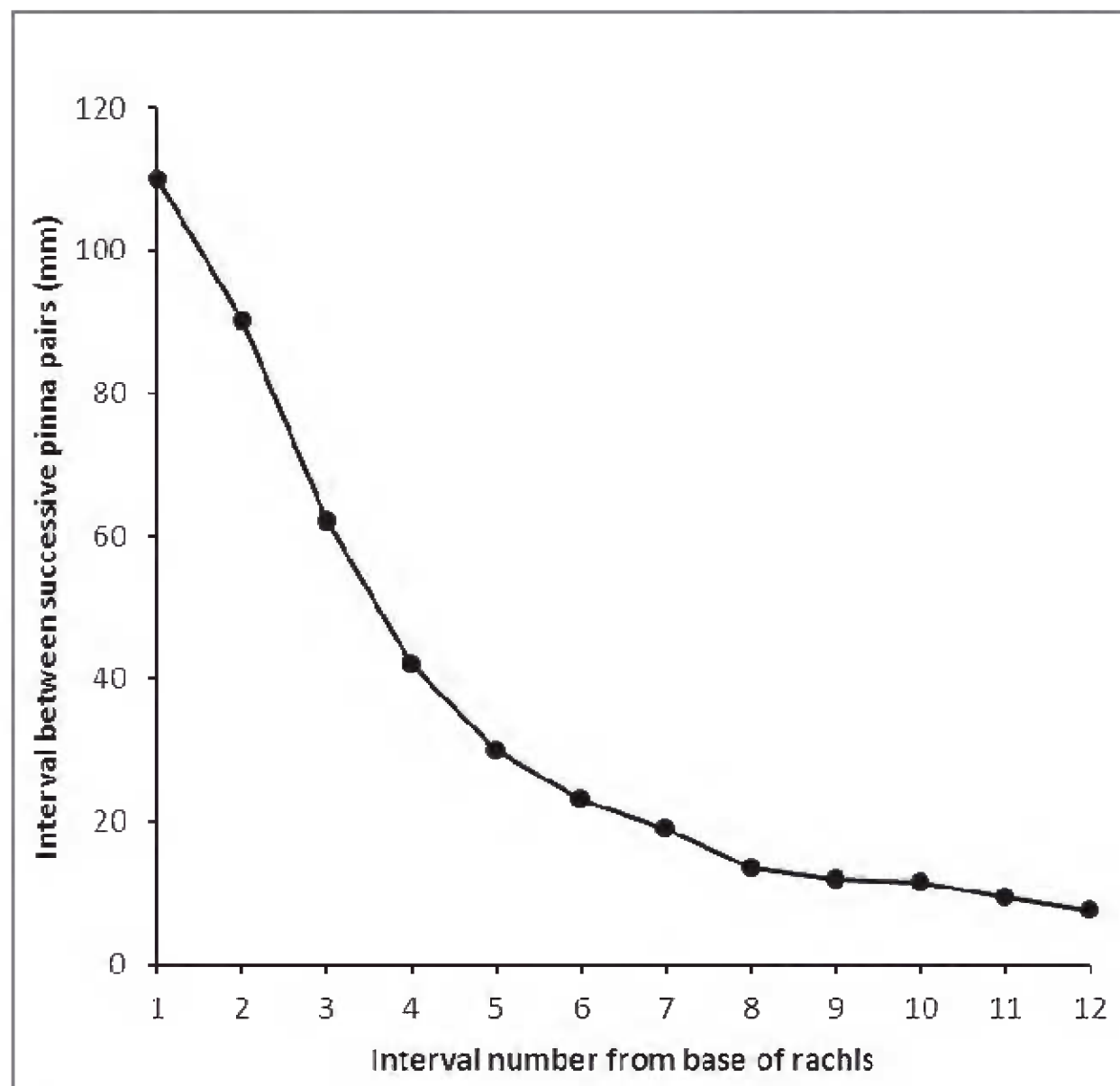|	Minimum	Median	Maximum
Length of lamina (mm)	341	676	1062
Basal free lobe on rachis (interval between costae)	8	11	13
Length of basal pinna (mm)	195	449	865
Basal free lobe on costa (interval between costules)	3	8	12
Length of basal pinnule (mm)	75	203	387
Basal free lobe on costule (interval between costulets)	1	2	7

Fig. 2. Spacing of successive pinna pairs (P1–P13) on the rachis of the frond of *P. esculentum* subsp. *esculentum* shown in Fig.1. Intervals 1 to 12 correspond with the distances P1 to P2, P2 to P3….P12 to P13 respectively.

Factors affecting expression of the free-lobe character

The association between the length of major laminal axes and the presence/absence of free lobes on their basal intervals in *P. esculentum* subsp. *esculentum* suggests involvement of environmental factors affecting plant form and growth, whereas the general pattern of pinna spacing on the rachis (see above) is maintained across wide variation in size and dissection of the lamina, as in *P. aquilinum* subsp. *aquilinum* (Bright 1928).

In *P. aquilinum* subsp. *aquilinum* Bright (1928) reported marked reductions in the number of pinnae, the length of the lowest pinnae and laminal size with increased exposure of stands to sunlight, wind and frost compared to fronds from more sheltered positions. Boodle (1904) had earlier noted more highly divided laminae in sheltered-form compared with exposed-form fronds in this subspecies. Boodle also observed that different leaves of the same plant grown consecutively in two different environments, or different portions of the lamina of a single frond, show changes over the same range when transferred between contrasting environments, indicating that such aspects of phenotype are determined only late in development.

O'Brien (1963) observed fronds of *P. esculentum* subsp. *esculentum* growing in protected situations to a height of 2.5 to 3 m, compared with average frond heights at the other extreme of 15 to 25 cm in stands growing on poor coastal soils and exposed to strong winds and full sunshine. Laminae were found to be markedly more divided in fronds from sheltered positions with good soil nutrition, shading from hot sunshine, protection from strong wind and adequate soil moisture than fronds from more exposed microhabitats. The scale of variation in such division under different growth conditions in subsp. *esculentum* is evident in comparison of the basal pinnulets of a basal pinna (Fig. 1) from a frond of average size collected in an open woodland stand, with a basal pinnulet (Fig. 3) from a basal pinna of a large shade-form frond over 3 m high growing in a contiguous moist gully microhabitat. This shade-form pinnulet exemplifies 4-pinnate to 4-pinnate-pinnatifid laminal subdivision in contrast to the pinnulets of the frond in Fig. 1 that show 3-pinnate to 3-pinnate-pinnatifid subdivision with free lobes only on the basal few intervals on the costule of basal pinnules. In the large pinnulet of Fig. 3, there is again a gradation in spacing of segment axes on the costulet repeating the general trend at all levels of laminal subdivision, but here on a small scale. Segments are contiguous at the apex of the costulet but are slightly more widely spaced in the central and proximal zones where long segment bases and free lobes respectively have formed (Fig. 3). If development is relatively slow as in cool shady conditions, there is

a reduced incidence of uncut long-adnate segment bases, laminal subdivision proceeds further (compare Figs 1 and 3), and typical lunate free lobes extend to more of the longer basal axial intervals. Conversely, relatively rapid development and frond expansion favours limited laminal subdivision (O'Brien 1963). This results in a higher incidence of axial intervals without free lobes and a relative increase in contiguous uncut adnate segment bases that contribute to a winged appearance in subapical axial intervals. Thus there are a number of indications that the rate of frond expansion defines a "window of opportunity" for the formation of free lobes. This model is consistent with Boodle's (1904) contention that laminal subdivision and other aspects of frond morphology are determined only late in the development and expansion of the bracken leaf. It is shown here that such morphological variability is restricted by over-riding control of the pattern of differential spacing of the laminal axes at each level.
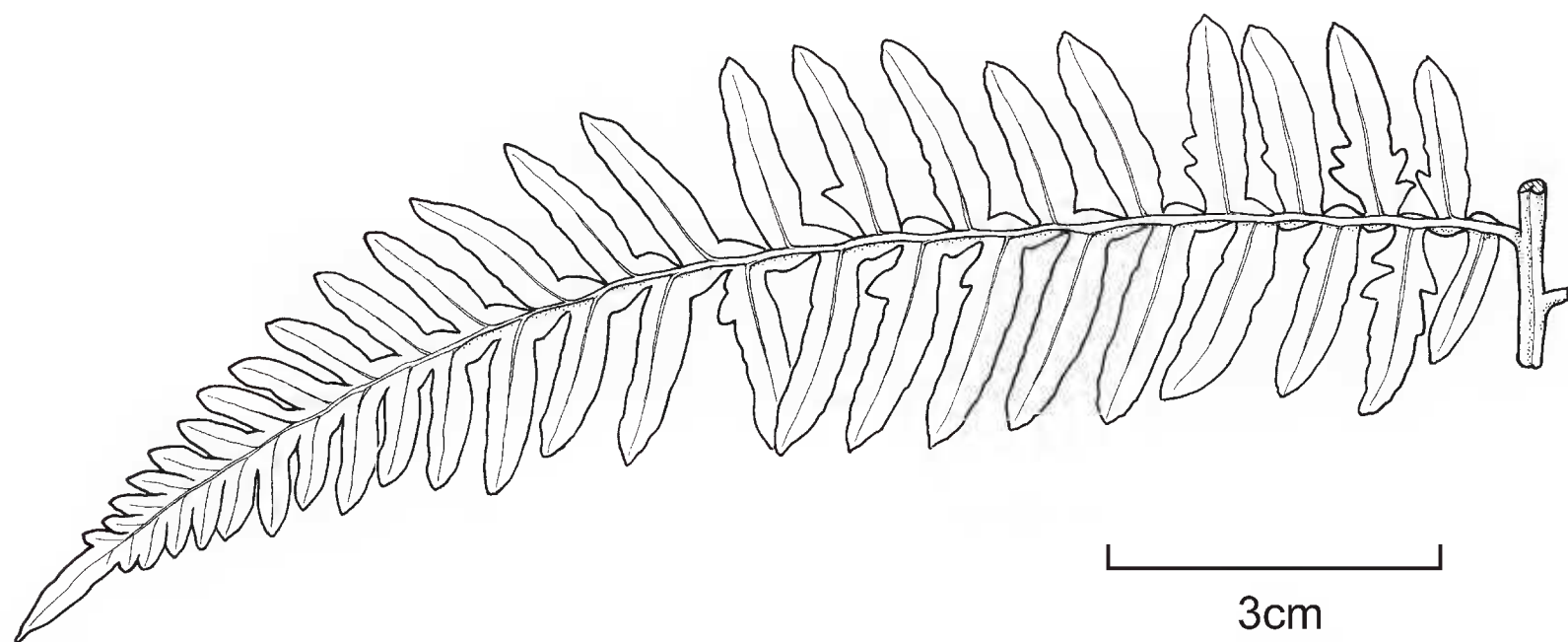

Fig. 3. Pinnulet of an exceptionally large sheltered-form frond of *P. esculentum* subsp. *esculentum* with 4 pinnate to 4-pinnate-pinnatifid laminal dissection showing free lobes on basal intervals of the costulet. Scale bar: 30 mm.

Genotypic basis of free-lobe expression

Detailed examination of the expression of free lobes is timely in view of a major recent study by Schwartsburd et al. (2014) who recognised three morphotypes in diploid South American brackens at subspecific rank within *P. arachnoideum* (Kaulf.) Maxon. These morphotypes are distinguished as showing (i) both free axial lobes and gnarled trichomes (morphotype "ined."), (ii) free axial lobes but not gnarled trichomes (morphotype "arachnoideum") or (iii) gnarled trichomes but not free lobes (morphotype "campestre"). Both morphotypes "arachnoideum" and "campestre" are apparently diploid based on stomatal guard-cell length (Schwartsburd et. al. 2014), as are many specimens of subsp. *arachnoideum* from Central and South America that have both free lobes and gnarled trichomes (Thomson 2000, Thomson and Alonso-Amelot 2002, Wolf et al. 2015). The study by Schwartsburd et al. (2014) was numerically large scale, established diploidy for a sample of the collections and revealed a coherent geographic distribution of sites for each morphotype. Considered together with the observation of an apparently diploid bracken accession with gnarled trichomes but without free lobes in the vicinity of typical subsp. *arachnoideum* in the Galapagos Islands (Wolf et al. 2015), these results suggest that a genetic presence/absence polymorphism may underlie this character. More large scale population studies of *P. esculentum* s.l. including genome size determination are required not only in the Galapagos Islands but also in Venezuela where Ortega (1990) reported a variant ecotype of subsp. *arachnoideum*. This variant form lacks free lobes and, perhaps significantly, shows unusually compact spacing of laminal axes, and may be of hybrid origin.

Conclusion

Development of free lobes in *P. esculentum* starts with extension basiscopically of an adnate lobe or wing of tissue decurrent to a simple distal segment proximal to the apex of the axis carrying it. As this axis extends, in successive intervals down it the greater part of the lobe becomes increasingly separated from the parent segment base as a lunate or semi-lunate portion of typical laminal tissue. The midrib of the segment that gave rise to this free lobe becomes the more apical of the two subordinate axes delimiting the axial interval to which that free lobe is attached. The basic hierarchy of spacing between the laminal axes at successive levels of blade dissection is similar in fronds of greatly different size. In contrast, the position of the most proximal

free lobes on the laminal axes is significantly correlated with the length of axial intervals which is mediated by environmental factors influencing growth rate and laminal subdivision.

Plants intermediate in morphology between *P. esculentum* s.l. and *P. aquilinum* s.l. have been widely reported (e.g. Tryon 1941, Mickel and Beitel 1988, Mickel and Smith 2004), especially in locations such as the Galapagos Archipelago (Wolf *et al.* 2015) and northern Australia (Brownsey 1989, 1998) and may include both allotetraploids and introgressants of other ploidy. Fully discrete free lobes appear to be absent in all specimens for which tetraploid status (4n = 208) has been supported by nuclear genome analysis, determination of nuclear DNA content or by comparison of stomatal guard cell lengths (Tan and Thomson 1990, Thomson 2000, Thomson and Alonso-Amelot 2002, Der et al. 2009, Wolf et al. 2015). Importantly, however, Brownsey (1989) has observed that free lobes appear reduced in number and demarcation in some of the putative hybrids that may be diploid, as for instance in those between *P. esculentum* subsp. *esculentum* and *P. aquilinum* subsp. *wightianum* (as *P. revolutum*) in which "…. the free lobes on the midribs of the primary or secondary pinnae are less numerous and clearly defined" than those of *P. esculentum* subsp. *esculentum*. An improved understanding of the form and placement of free lobes should facilitate more positive identification of such hybrids, their parents, and their possible introgressants as, for example, in the Galapagos Islands (Wolf et al. 2015) and northern Australia. Clarification of recognition criteria for free axial lobes also contributes to validation of their potential use as a presence/absence polymorphism providing a genetic marker in further population and biogeographic studies building on the work of Schwartsburd et al. (2014).

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